

DEMOGRAPHY OF THE ENDANGERED PLANT,
SILENE SPALDINGII (CARYOPHYLLACEAE) IN
NORTHWEST MONTANA

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ABSTRACT

I conducted a demographic study of the endangered perennial herb, *Silene spaldingii*, following >170 mapped individuals from 1987 through 1996 on a preserve in northwest Montana. *Silene spaldingii* occurs in mesic sites, but highest densities are negatively correlated with the density of the largest bunchgrass, suggesting that disturbance may play a positive role in the species' life history. Equilibrium population growth was stable over the period of the study, although significant recruitment occurred in only two of the seven years for which it could be accurately measured. *Silene spaldingii* is a long-lived perennial, with 72% of the plants observed in 1989 still present in 1994. Plants spent nearly 50% of their summers in a dormant condition, and this appears to be an important life history strategy in this semi-arid environment. Flowering, recruitment, and growth were positively correlated in time, and all were negatively correlated with summer dormancy. These demographic parameters were correlated only with mean winter temperature; however, they exhibited two-year cycles, suggesting that plants may be strongly influenced by their previous-year performance. Prescribed fire may be a useful tool for managing *S. spaldingii* at this site.

Silene spaldingii is a perennial herb endemic to the Palouse region of southeast Washington and adjacent Oregon and Idaho and is disjunct in northwest Montana (Hitchcock and Maguire 1947). Much of the habitat of *S. spaldingii* has been lost to agricultural development. Although once widespread in the Palouse region, *S. spaldingii* is now known from ca. 60 mainly isolated sites on the periphery of its former range. Most remaining populations are small and threatened by exotic weed encroachment, livestock grazing, and herbicide treatment (Gamon 1991; Lorain 1991; Schassberger 1988). *Silene spaldingii* is listed as threatened or endangered in all four states in which it occurs (Lesica and Shelly 1991).

Knowledge of demographic patterns is essential to understanding population dynamics. Estimates of vital rates, such as recruitment, growth, and mortality, obtained from demographic studies form the basis for predictions of future population growth (Menges 1990; Schemske et al. 1995). Correlations between demographic parameters and environmental variables such as climate and disturbance events can also provide insights into population dynamics and life history (Menges 1990; Schmalzel et al. 1995). Demographic studies are especially important for developing conservation management

plans for threatened species (Menges and Gordon 1996; Schmalzel et al. 1995).

The largest known population of *S. spaldingii* occurs at The Nature Conservancy's Dancing Prairie Preserve in northwest Montana. Management options such as fire are being considered for the preserve. The purpose of my study was to describe the habitat and demography of *S. spaldingii* on the preserve and to use this knowledge to help determine the long-term fate of the *S. spaldingii* population on the preserve and make recommendations regarding management.

METHODS

Species description. *Silene spaldingii* S. Watson (Caryophyllaceae) is a partially self-compatible, hermaphroditic, perennial herb, 20–40 cm tall, with a simple or branched caudex surmounting a long, slender taproot. Rhizomes or other means of vegetative propagation are lacking (Hitchcock and Maguire 1947; Lesica personal observation). Three to 20 flowers are borne in a branched terminal inflorescence. Flowers are pollinated mainly by bumblebees (Lesica 1993; Lesica and Heidel 1996), and fruit capsules mature in August. Seeds germinate with as little as four weeks of cold treatment (Lesica 1993), so germination probably occurs in fall as well as spring. Rosettes are formed the first year, after which vegetative stems are produced. Flowering usually does not occur until during or after the third season (see Results).

Study site. Dancing Prairie Preserve is ca. 300 ha in a narrow glacial valley at 825 m, 6 km north of Eureka in northwest Montana (T37N R27W S26). At Fortine, ca. 27 km south and 75 m higher, mean annual precipitation was 438 mm for 1950–1980. Mean July maximum and January minimum were 27.9° and –11.4°C respectively. *Silene spaldingii* occurs most commonly in shallow swales with deep soil dominated by large bunchgrasses (see Lesica 1993 for further details). The area had been grazed by domestic cattle, but grazing ceased when the preserve was established in 1987.

Associated vegetation. On 15–16 July 1991, after growth of dominant grass species had ceased, I established 30 113-m² (6 m radius) circular plots throughout the portion of the preserve where *S. spaldingii* occurs. I located plots so that each would contain at least ten plants of *S. spaldingii*; otherwise plot location was random. For each plot, I ocularly estimated canopy cover of all vascular plant species to the nearest 5% and recorded the size of each *S. spaldingii* plant and total density. I used principal components analysis of dominant plant cover and total plant, grass, and forb cover followed by a Pearson correlation analysis of principal components (PC) to explore

biological factors that may affect the density of *S. spaldingii* at Dancing Prairie Preserve.

Demography and life history. In mid-July 1987, four permanent monitoring transects were established in different parts of the preserve where *S. spaldingii* occurs. Transects were located subjectively to represent the population and were read annually in late July through mid-August through 1996. Each transect consisted of 40–50 adjacent 1-m² mapping quadrats placed along the transect line (Lesica 1987). The position of each *S. spaldingii* plant encountered in the quadrats was mapped and classified by growth form, reproductive status, and fecundity using the following classification:

Seedling — rosette, lacking any visible stem elongation

Dormant — no above-ground parts observed

Non-reproductive — one or more stems present but no flowers

Reproductive — one or more fertile stems present. The number of flowers was recorded for each reproductive plant.

Data analysis. *Silene spaldingii* plants may go undetected for one to several years but reappear in subsequent years (Lesica and Steele 1994). The presence of summer dormant plants can be inferred by comparing transect maps from the full sequence of years. A small proportion of these dormant plants produce small leaves that senesce and disappear by early July, while the remainder remain underground for the entire growing season (see Results). Prolonged dormancy made exact estimation of many demographic parameters difficult; however, by eliminating the initial and final two years of data, acceptable levels of error can be achieved (see Results). Plants that failed to reappear for three consecutive years were assumed dead.

Growth was defined as the proportion of plants in year t that moved to a larger size class in year $t + 1$. For analysis of growth, reproductive plants were divided into two size classes: those with <10 and those with ≥ 10 flowers. Flowering was defined as the proportion of reproductive plants. Recruitment was measured as the ratio of recruits in year $t + 1$ to reproductive plants in year t . Fecundity was measured as the number of flowers per reproductive plant. Half-life was calculated as $t \ln 2 / \ln N_x - \ln N_{x+t}$ where N_x was the number of plants at time x and N_{x+t} was the number after t years (Silvertown 1982). Pearson's correlation coefficients between mean temperature and precipitation for summer (Jul–Sep), fall (Oct–Dec), winter (Jan–Mar), and spring (Apr–Jun) and demographic parameters of the subsequent flowering season were calculated. Weather data were relativized to their overall means before analysis.

Stage-structured transition matrix projection models summarize the way in which survival, growth, and reproduction at various life-history stages interact to determine population growth (van Groe-

nendaël et al. 1988; Caswell 1989), and they can be used to summarize short-term population dynamics (Caswell 1989). There are two ways in which a reproductive plant can undergo a transition: the plant survives (Rep column) or the plant produces progeny in the rosette or vegetative classes (Rec column). The separation of these two components of reproductive transition causes an asymmetrical matrix with an extra column. The two probabilities (Rep, Rec) but must be added together in order to solve for λ . Equilibrium growth rate (λ) is the dominant eigenvalue of the transition matrix (Caswell 1989; Lefkovitch 1965). $\lambda > 1.0$ indicates population increase, while $\lambda < 1.0$ indicates decrease. λ integrates the effects of survival, growth, and fecundity of the different life-history stages into a single parameter. Details on the construction and use of matrix population models can be found in Caswell (1989) and Menges (1990).

Elasticity measures the relative change in the value of λ in response to changes in the value of a transition matrix element. Elasticity matrices allow comparison of the relative contributions of various life history transitions to population growth and fitness (de Kroon et al. 1986). Elasticities sum to unity, and regions of the matrix may be summed to compare the importance of growth and survival to recruitment (Caswell 1989).

The sporadic recruitment of rosette-class plants into the sample population precludes solving most 1-year matrices. In order to assess the population growth of the Dancing Prairie *S. spaldingii* population for 1989–1994, a “summary” matrix was constructed by summing 1-year frequency tables for the period (Caswell 1989, p. 81). This method of obtaining a multi-year estimate of population growth tends to obscure the multiplicative effects of year-to-year differences in population growth. However, a summary matrix allows multi-year assessment of elasticity.

The character of the *S. spaldingii* seed bank at Dancing Prairie is not known. Not including a seed bank in the matrix model may affect the value of λ (Kalisz and McPeck 1992), especially when it is lower than 1.0. However, it will have little effect on the analyses based on elasticities (Silvertown et al. 1993). I calculated separate elasticities for reproductive transitions and recruitment by dividing the reproductive + recruitment elasticities proportionately between the two components.

RESULTS

Associated vegetation. Vegetation supporting colonies of *Silene spaldingii* was dominated by *Festuca scabrella* (canopy cover = 70%), *F. idahoensis* (17%), and *Poa pratensis* (7%); *Antennaria microphylla* (3%), *Arnica sororia* (4%), and *Hieracium cynoglos-*

soides (3%) were common forbs. The first principal component accounted for 38% of the variance in the data and represented a gradient of increasing plant cover, especially forbs but excluding *Festuca scabrella*. The second principal component accounted for 27% of the variance and was associated with increasing cover of *F. scabrella* and decreasing cover of *Poa pratensis*. Density of *S. spaldingii* was positively correlated with PC 1 ($r = 0.43$, $P = 0.019$), and density of large (≥ 10 flowers) *S. spaldingii* plants was negatively correlated with PC 2 ($r = -0.45$, $P = 0.014$).

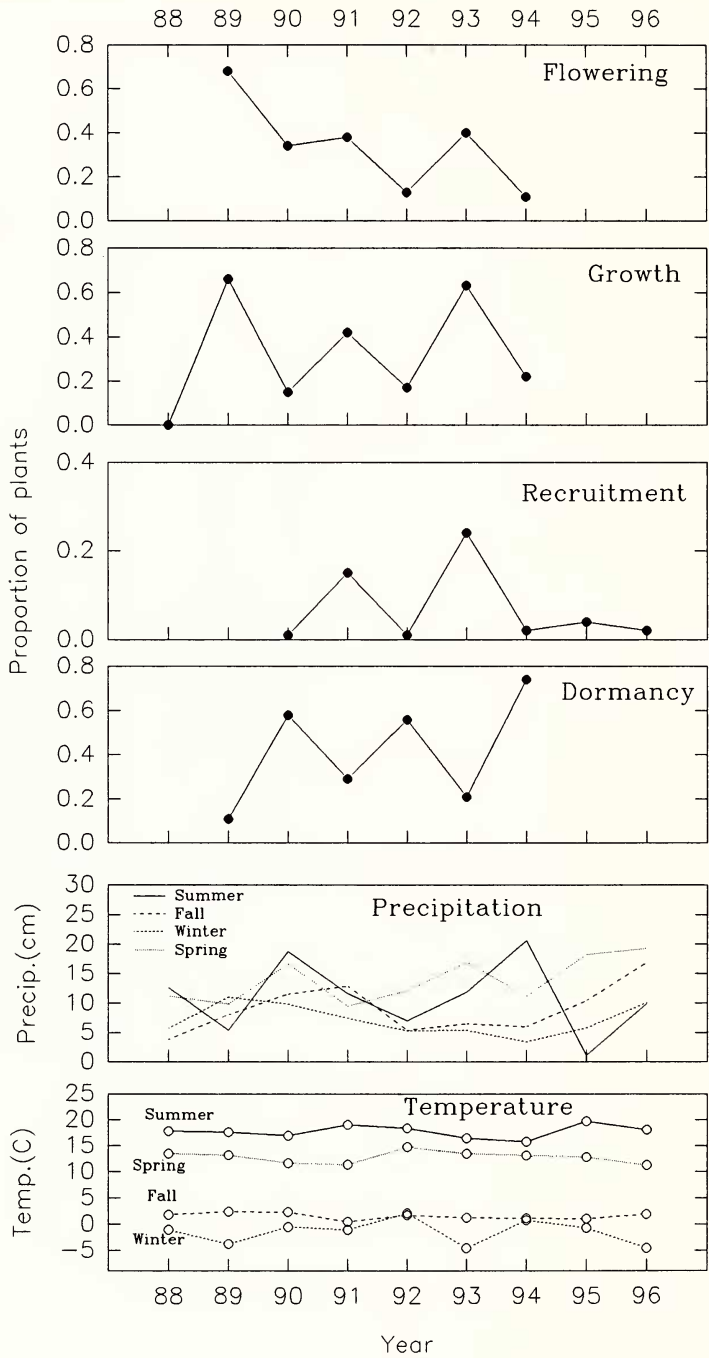
Prolonged dormancy. *Silene spaldingii* plants were not apparent above ground on 8 May 1996, but were apparent by 22 May 1995. Of the 67 plants recorded as not present in July 1995, seven (10%) were recorded in May of the same year, indicating that ca. 10% of plants assigned to the dormant size class produced short-lived, above-ground vegetation early in the growing season, while the remaining 90% did not.

A mean of 41% (SE = 10%) of *Silene spaldingii* plants exhibited summer dormancy annually from in 1989–1994, ranging from 11% in 1989 to 74% in 1994 (Fig. 1). Of the 193 episodes of prolonged dormancy recorded during this period, 75% were one year in duration, and 90% were either one or two years long. Thus, only ca. 4% ($10\% \times 41\%$) of *S. spaldingii* plants were undetected by the third year of the study (1989). The mean number of summers of dormancy for plants that persisted between 1989 and 1994 was 2.65 (SE = 0.15, $N = 72$), indicating that plants spent nearly half of their summers in dormant condition.

Growth. The percentage of plants moving into a larger size class compared to the previous year varied from 0% in 1988 to 66% in 1989 (Fig. 1).

Survivorship. The exact year that a *S. spaldingii* plant dies is difficult to ascertain because of prolonged dormancy. A plant may be dormant in year t and die in year $t + 1$, but it would appear that death occurred in year t . Fortunately, this problem does not affect the calculation of half life and has only a small effect on the shape of depletion curves.

Seventy-two percent of the plants observed in 1989 were still alive in 1994 (Fig. 2). Mortality appeared to be episodic; 22 of the 28 deaths probably occurred between the 1989 and 1990 censuses, and 15 of these occurred in adjacent quadrats of transect 4. The causes of mortality are not known. Half-life of the 1989 uneven-age cohort was 12 years, and of the 13 plants recruited in 1991, at least 9 (69%) were still alive in 1996, most mortality occurring in the first year (Fig. 2).



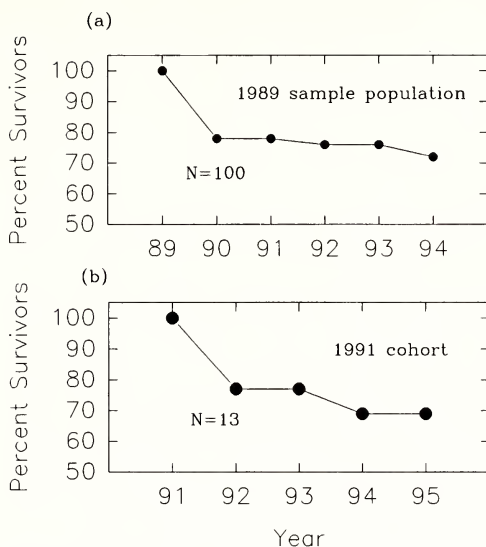


FIG. 2. (a) Depletion curve for *Silene spaldingii* sample population. (b) Survivorship curve for *S. spaldingii* cohort recruited in 1991.

Recruitment. Significant recruitment was episodic, occurring in two of the seven years in 1990–1996 (Fig. 1). Thirteen non-reproductive plants appeared in 1991, while 19 rosettes and 6 non-reproductive appeared in 1993.

Flowering. The percentage of plants flowering in 1989–1994 varied from 11% in 1994 to 68% in 1989 (Fig. 1). Twenty-six plants were recruited in 1993, and of the 17 that lived until 1996, six flowered in 1995 and an additional two flowered in 1996.

In 1987–1996, the mean number of flowers per reproductive plant was 6.11 (SE = 0.24) and varied between 3.94 in 1996 and 7.84 in 1990. The difference among years was significant (ANOVA; $F = 2.01$, $P = 0.04$, $N = 356$). Fecundity was not strongly correlated with any weather variable ($r < 0.28$). Plants with multiple flowering stems were rare throughout the study ($< 7\%$, $N = 372$).

Life history and weather correlations. Flowering, recruitment, and growth were positively correlated among years, and dormancy was negatively correlated to all three (Fig. 1, Table 1). These four demographic parameters all demonstrated a strong biennial periodicity

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FIG. 1. Demographic parameters (see Methods for definitions) for *Silene spaldingii* and annual seasonal temperature and precipitation in 1988–1996.

TABLE 1. PEARSON'S COEFFICIENTS FOR CORRELATIONS BETWEEN PARAMETERS OF *SILENE SPALDINGII* DEMOGRAPHY AND CLIMATE: FLOW (PROPORTION PLANTS IN FLOWER), DORM (PROPORTION PLANTS DORMANT), RECT (RECRUITMENT), GRTH (GROWTH), WNPR (WINTER PRECIPITATION), SUPR (SUMMER PRECIPITATION), AND WNTM (MEAN WINTER TEMPERATURE). Significant coefficients (single-test $P \leq 0.05$) are in bold; parameters without one coefficient >0.70 ($P = 0.12$) are not included.

	Flow	Dorm	Rect	Grth	Wnpr	Supr
Dorm	-0.82	—	—	—	—	—
Rect	0.73	-0.92	—	—	—	—
Grth	0.66	-0.88	0.99	—	—	—
Wnpr	0.81	-0.53	-0.18	0.36	—	—
Supr	-0.50	0.70	-0.05	-0.45	-0.33	—
Wntm	-0.83	0.85	-0.56	-0.78	-0.43	-0.21

that does not appear to be related to any weather variable examined, except perhaps winter temperature (Fig. 1). Mean winter temperature was strongly correlated with flowering (-), growth (-), and dormancy (+). Winter rain was correlated only with flowering (+), and summer rain was correlated only with dormancy (+) (Table 1).

Population growth and elasticity. The summary projection matrix for 1989–1994 is presented in Table 2a. Population growth rate (λ)

TABLE 2. (a) SUMMARY STAGE-BASED TRANSITION MATRIX FOR *SILENE SPALDINGII* IN 1989–1994. The Rep (reproductive) and Rec (recruitment) columns must be added together before solving for λ , the dominant eigenvalue (see Methods). Other classes are Ros (rosette), Dor (summer dormant), and Veg (non-reproductive stems). (b) MEAN ELASTICITIES FOR ABOVE STAGE TRANSITION MATRIX. The left three columns represent nonreproductive growth and survival. The reproductive column represents growth and survival of reproductives. The recruitment column represents recruitment from seed.

	From				
	Ros	Dor	Veg	Rep	Rec
(a)					
To					
Ros	0.045	—	—	—	0.097
Dor	0.727	0.433	0.398	0.558	—
Veg	—	0.228	0.219	0.170	0.112
Rep	—	0.339	0.281	0.160	—
$\lambda = 1.00$					
(b)					
To					
Ros	0.001	—	—	—	0.020
Dor	0.020	0.207	0.095	0.153	—
Veg	—	0.097	0.047	0.042	0.027
Rep	—	0.171	0.071	0.046	—

was 1.00, indicating that the sample population of *S. spaldingii* was stable during this time period.

Elasticity gives the proportional importance of demographic transitions to population growth. An elasticity matrix for 1989–1994 is presented in Table 2b. There were three important transitions: (1) reproductive to dormant, (2) dormant to reproductive, and (3) dormant to dormant. These sum to greater than 50%. The sum of recruitment into the rosette and non-reproductive size classes was less than 5%.

DISCUSSION

Silene spaldingii occurs only in relatively mesic areas dominated by *Festuca scabrella* at Dancing Prairie Preserve. Within these areas, however, density and flowering of *S. spaldingii* plants are associated with lower dominance of *F. scabrella*. *Festuca scabrella* is very productive compared to *F. idahoensis* and *Poa pratensis* (Mueggler and Stewart 1980) and produces large amounts of litter annually. Litter produced by dominant plants may inhibit growth and reproduction of subordinates (Bergelson 1990; Tilman 1993), and many species require disturbances such as fire in order to persist (Hardin and White 1989; Parsons and Browne 1982). Results of the vegetation analysis support the hypothesis that *S. spaldingii* reaches its greatest abundance in sites with reduced interference from the dominant grass. Thus, disturbances such as grazing or fire may be important to the long-term persistence of this species in northwest Montana.

Silene spaldingii is a long-lived perennial. The depletion curve declines very gradually with 72% of plants surviving for at least 5 years. Furthermore, survival of first-year plants is high, indicating that most mortality occurs in early seedling stages, before July censuses. The majority of adult mortality occurred in one transect in one year. Although the cause of these deaths is not known, it appears that major causes of mortality in the sample population were environmental or catastrophic rather than demographic or genetic (Shaffer 1981). Low but temporally and spatially variable mortality also characterized *S. douglasii* populations in Oregon (Kephart and Paladino 1997).

Recruitment of *S. spaldingii* was sporadic, occurring primarily in two of the seven years for which it could be measured. Unfortunately, I was unable to detect any climatic correlates with recruitment. It is common for herbaceous perennials to exhibit irregular recruitment (Harper 1977, Chapter 19). In spite of episodic recruitment and apparently catastrophic mortality, population growth rate for *S. spaldingii* was 1.00 for 1989–1994, indicating that the sample population was stable.

Prolonged dormancy plays an important role in the life history of *S. spaldingii*. Most plants spent nearly half of their summers in dormant condition. Elasticity analysis suggests that more than 50% of population growth in this stable population was due to survival and growth of plants in the dormant stage. There was a tendency for summer dormancy to be more common when preceded by a warm, dry winter. *Silene spaldingii*'s long, deep-seated taproot undoubtedly acts as a storage organ, allowing dormancy when producing above-ground organs is not advantageous.

Flowering, growth, and recruitment were all temporally correlated, and all three of these were negatively correlated with the occurrence of prolonged dormancy. 'Favorable' years for *S. spaldingii* with high flowering, growth, and recruitment and infrequent summer dormancy occurred in 1989, 1991, and 1993. Mean winter temperature was the only weather variable strongly correlated with these demographic parameters. It is not known why cold winters should be followed by high levels of growth and flowering in *S. spaldingii*. The lack of understandable correlations with weather variables and the two-year periodicity of demographic parameters suggests that performance in one year may impact performance in the subsequent year (Sork et al. 1993). Models of mast-fruitletting suggest that members of a population with physiological constraints promoting periodic fruitletting are synchronized by an extreme weather event (Silvertown 1980; Waller 1993). A similar explanation could account for the demographic patterns observed in the Dancing Prairie *S. spaldingii* population.

MANAGEMENT CONSIDERATIONS

Fire may be important for the long-term persistence of *S. spaldingii* in highly productive grasslands like those in northwest Montana. Many rare and endangered plant species require natural disturbance regimes to persist (Bowles et al. 1990; Hardin and White 1989; Parsons and Browne 1982). Fire is thought to play an important role in recruitment of *Silene regia*, a congener of eastern North American prairies (Menges 1995). Vegetation association data suggest that *S. spaldingii* could maintain larger populations where disturbance reduces litter produced by the dominant grasses. Prior to establishment of the preserve in 1987, moderate livestock grazing undoubtedly helped reduce the levels of plant litter. However, grazing by large herds of ungulates was uncommon in the bunchgrass-dominated grasslands and steppes of presettlement Intermountain Western North America (Mack and Thompson 1982), so fire was likely the predominant disturbance (Arno and Gruell 1983; Daubenmire 1970). Recruitment of *Silene spaldingii* is sporadic, perhaps depending on climate or disturbance episodes. However, it is a long-

lived perennial, enabling populations to persist many years without recruitment, so prescribed fire intervals need not be very frequent.

Results obtained from Dancing Prairie, at the extreme edge of the range of the species, cannot necessarily be extrapolated to populations remaining in the Palouse region, because demographic patterns may change with location and habitat (Kephart and Paladino 1997; Lesica and Shelly 1995). Fire should not be reintroduced at Dancing Prairie without further study. Disturbance may have adverse effects, such as exotic weed encroachment, even in fire-adapted systems (Hobbs and Huenneke 1992). Furthermore, the effect of fire on *S. spaldingii* may depend on season of burn (Howe 1994). The effects of fire on *S. spaldingii* population dynamics and on local weed populations are being investigated at Dancing Prairie Preserve.

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